

the assimilation of nutrient from this dietary fiber. Thus, in a study on efficiency of food utilization MARTINO (2000) found that in spite of the high fiber/protein ratio of *B. unioloides* its apparent digestibility (NDF) was high ( $0.81 \pm 0.04$ ). Selection of grasses was also reported for the rodent *Lagostomus maximus* by BRANCH et al. (1994). Assuming food quality is correlated with the amount of annual forbs in the diet, these authors suggested, that grasses may provide essential dietary fiber to maintain caecum motility and the appropriate microbial environment in the hindgut. According to optimal-foraging models, plant defenses (e.g., structural, digestive-inhibiting chemicals, toxic chemicals, and nutri-

tional content) may be effective in reducing their intake by mammalian herbivores (BELOVSKY and SCHMITZ 1994). For example, *Hydrocotyle bonariensis*, which was not preferred by *C. talarum*, belongs to a genus known to contain relatively high concentrations of phytotoxins (JUSCAFRESA 1975).

## Acknowledgements

This research was granted by UNMdP subs. N° 2; Agencia Nacional de Promociones Científicas y Tecnológicas subsidio N° 01-00000-01348, CONICET-PEI-N° 6429. We thank two anonymous reviewers for giving constructive comments on earlier versions of the manuscript.

## Zusammenfassung

### Auswahl und Bevorzugung von Nahrung bei *Ctenomys talarum* (Tuco-Tuco)

In der Studie wurde die Auswahl und die Bevorzugung von Futterpflanzen bei *C. talarum* untersucht. Um die Auswahl zu schätzen wurde die oberirdische Biomasse der Futterpflanzen bestimmt, und die Zusammensetzung der Nahrung im Mageninhalt mittels mikrohistologischer Technik geschätzt. Die Bevorzugung von Futterpflanzen wurde mit Cafeteria-Experimenten im Laboratorium untersucht. *C. talarum* verhielt sich als ein Generalist und Opportunist durch Nutzung der meisten Arten, ändert die Nahrungswahl aber gemäß Verfügbarkeit. Oberirdische Pflanzenteile wurden gegenüber unterirdischen Teilen oder Blüten bevorzugt. Gräser bildeten 94% der oberirdischen Teile. Die Nahrung vom Tuco-Tuco variierte zwischen den Geschlechtern. Männchen verhielten sich selektiver als Weibchen. Die Cafeteria-Experimente zeigten auch, daß *C. talarum* oberirdische Teile der Gräser gegenüber den übrigen bevorzugt.

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## Short communication

# Bullate stapedes in some phalangeriform marsupials

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Receipt of Ms. 06. 10. 2000

Acceptance of Ms. 12. 12. 2000

**Key words:** Marsupialia, possums, ossicles, stapes, ear

Stapes form varies considerably among mammals and has been a disputed topic in morphology-based mammalian systematics (NOVACEK and WYSS 1986; ROSE and EMRY 1993; GAUDIN et al. 1996). One particular specialization that has received recent attention (WILKINS et al. 1999) is the bullate form of the stapes' footplate. A bullate stapes possesses 'a highly convex hollow footplate that protrudes into the vestibule of the inner ear' (WILKINS et al. 1999), instead of being flat or nearly flat like in most mammals. This situation was first reported by HYRTL (1845) for the common ring-tailed possum *Pseudocheirus peregrinus* (= '*Phalangista cooki*', Petauridae, Marsupialia). Subsequent to this work, other authors have described this anatomical specialization in several phylogenetically distant eutherian mammals (DORAN 1878; SEGALL 1971; BURDA et al. 1992; WILKINS et al. 1999 and references therein). Contrary to the statements of WILKINS et al. (1999), *P. peregrinus* is not the only marsupial showing a bullate stapes. SEGALL (1971) reported (but did not illustrate) this for the feathertail glider, *Acrobatodes pygmaeus* (Acrobatidae, Diprotodontia).

During the course of our studies on the evolution of ear ossicles in marsupials, we examined the stapes in more than 70 specimens representing 26 species in eight

'families'. In all cases the stapedial footplate was flat and not bullate, with the following three exceptions (Fig. 1): the brush-tailed opossum, *Trichosurus vulpecula* (n = 13); the grey cuscus, *Phalanger orientalis* (n = 2); and the spotted cuscus, *Spiloglossus maculatus* (n = 1). Of these three taxa, *T. vulpecula* shows this feature most marked, followed by *S. maculatus*. In *T. vulpecula*, the depth of the footplate equals that of the crural portion of the stapes, while in the other two taxa the proportion is smaller.

Some other marsupial taxa in addition to those mentioned above have a somewhat bullate stapes. SEGALL (1971: 34) reported that in *Petaurus norfolcensis* 'the vestibular surface of the plate is only slightly convex.' FLEISCHER (1973: 142) noted in his description of the stapes of *Petaurus breviceps* that '... seine Basis ist geringfügig ins Vestibulum vorgewölbt.' The condition in these species of *Petaurus* approximates that described here for *Phalanger orientalis*, as confirmed by examination of a specimen of *Petaurus breviceps* (SM-64418). Several eutherians have a convex footplate that approximates the bullate condition, e.g. *Sus* and *Cynocephalus* (DORAN 1878; ROSE and EMRY 1993). These cases illustrate well the fact that the definition of a bullate stapes is to some extent a matter of evaluation.

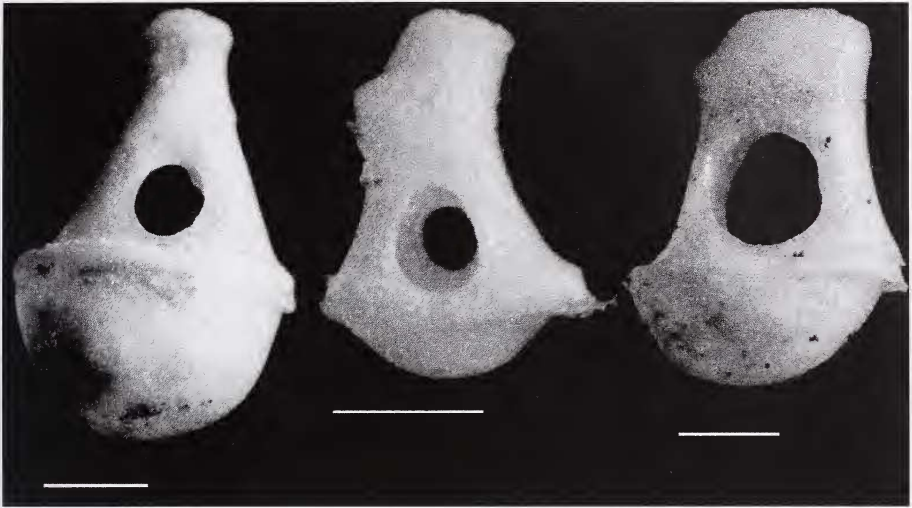


Fig. 1. Stapes of left) *Trichosurus vulpecula* (WM-pers.coll.) center) *Phalanger orientalis* (SM-54981) and right) *Spilocuscus maculatus* (SM-5610). Scale = 0.5 mm.

All the marsupial taxa for which a bullate stapes is reported here and elsewhere are phylogenetically close and taxonomically ordered within the Phalangeriformes (KIRSCH et al. 1997). The stapedes of other members of this group were studied by SEGALL (1971), including *Pseudocheirus herbertensis*, *Petauroides volans*, and *Dactylopsila trivirgata*, and in no case did this author mention any peculiarity in their stapes. Plotting the distribution of bullate stapedes in the phylogenetic tree of Phalangeriformes based on DNA-hybridization studies by KIRSCH et al. (1997), it is obvious that the bullate condition (at least in its marked form) has either evolved independently in several taxa, or has been lost independently if present in the last common ancestor of *Acrobates* and the other Phalangeriformes.

In addition to the adult macerated skulls, we examined histologically prepared specimens of several South American and Australasian marsupial taxa. Most species are represented by pouch-youngs, in some cases complete developmental series were examined (for a complete list, see SÁNCHEZ-VILLAGRA 2001). Among the species showing bullate stapes as adults, *T. vulpecula* was represented by two specimens.

An early pouch-young of *Trichosurus vulpecula* shows already a prominently outbulging footplate of the stapes that protrudes into the inner ear (Fig. 2), a condition that persists in the adult. Of all other taxa examined, only an early pouch-young of the eastern quoll, *Dasyurus viverrinus* also shows this condition. Adults of this species, as well as other adults of the Dasyuromorpha (ARCHER 1976) do not show this feature. For comparison, a pouch-young of *Perameles* sp. with the plesiomorphic marsupial condition of the stapes' footplate is shown in figure 2. In the specimens illustrated, the ear ossicles are in a blastemous, pre-cartilaginous stage. Much remodeling and growth takes place in the ear ossicles between these stages and adulthood.

The eutherians showing the most pronounced bullate stapes are rodents belonging to the Heteromyidae and Geomyidae, with highly derived middle ears and specialized to low-frequency hearing. Of all marsupials possessing bullate stapedes, only for *Trichosurus vulpecula* there has been an (electrophysiological) audiogram published (GATES and AITKIN 1982). Even though *T. vulpecula* does not have similar hearing abilities to those of the desert rodents mentioned above, an interesting departure from the few other marsupials (phylogenetically